Jackson, R. R. 1980. The mating strategy of *Phidippus johnsoni* (Araneae, Salticidae): II. Sperm competition and the function of copulation. J. Arachnol., 8:217-240.

THE MATING STRATEGY OF *PHIDIPPUS JOHNSONI* (ARANEAE, SALTICIDAE): II. SPERM COMPETITION AND THE FUNCTION OF COPULATION

Robert R. Jackson [1]

Department of Zoology
University of California
Berkeley, California 94720

ABSTRACT

The number and sequence of individual palp applications during copulation were highly variable. Copulation duration was correlated with different mating tactics: a. adult female outside nest, type 1 courtship (vision dependent), copulate outside nest (mean duration: 14 min); b. adult female inside nest, type 2 courtship (vibratory), copulate inside nest (110 min); c. subadult female inside, cohabitation, copulate inside nest after maturation of female (863 min). Females were more likely to oviposit fertile eggs after long copulations; but given that any fertile eggs were oviposited, there was no evidence that the number varied with copulation duration. Female fidelity (the probability that she would not mate when another male courted her) was greater after longer copulations. When females became unreceptive after mating, the effect was nearly immediate. Males covered the copulatory orifices of females with mating plugs that apparently hindered insemination attempts by later males. Females that mated with more than one male included some that were capable of ovipositing fertile eggs after their first copulation. The sterile male technique (x-radiation) was used to investigate the consequences of repeated mating. Sometimes the second male failed to displace any of the first male's sperm. Other times, there was partial or complete displacement. Possible mechanisms controlling female receptivity and their adaptive significance are discussed.

I. INTRODUCTION

Very lengthy copulations occur in many animal groups. For example, some species of crustaceans and insects may remain *in copula*, without interruption, for hours or even weeks at a time (Hartnoll 1969, Nayar 1958, Richards 1927, Unwin 1920). At the opposite extreme, copulation lasts for only a few seconds in some Diptera (Corbet 1964, Syrjamaki 1966). Comparable variance among species occurs in the copulation durations of spiders (Bristowe 1958). There is also variation among species in the details of copulatory behavior. For example, there may or may not be repeated mounting or the formation of locks; and the male and female may assume various positions relative to each other, such as facing the same or opposite directions and the male dorsal or ventral to the female (Gerhardt and Kaestner 1937, Richards 1927). To understand interspecific variation in copulatory behavior apparently requires consideration of functions in addition to the simple transfer of sperm from the male to the female.

[1] Present Address: Department of Zoology, University of Canterbury, Christchurch 1, New Zealand.

In species in which females copulate with more than one male, sperm competition often occurs (Parker 1970). In competition of this type, the female's eggs are a limited resource for the males. As the proportion of her eggs fertilized by one male's sperm increases, the proportion fertilized by the sperm of other males decreases. Many aspects of the reproductive biology of animals can be viewed as adaptations related to this type of competition. Although sperm competition has rarely been considered in studies of spiders, arguments concerning particularly intense sperm competition in insects probably apply to spiders as well, since a single male ejaculate may be adequate to match the female's semen storage capacity and fertilize all her eggs.

In the salticid spider *Phidippus johnsoni* Peckham and Peckham, there is a surprising degree of intraspecific variation in copulatory behavior. In particular, the duration of copulation varies within this species over a range approaching that which occurs in the animal kingdom as a whole. This extraordinary variance in copulation duration is correlated with the alternative mating tactics employed by the males of this species (Jackson 1977a):

(1) Courtship occurring outside the nest tended to be followed by copulations lasting only a few minutes.

(2) Courtship involving females encountered as adults inside nests tended to be followed by copulations inside nests lasting as long as several hours.

(3) Following cohabitation, copulations with newly matured females tended to be extremely lengthy, frequently lasting longer than a day.

Previously the pursuit times (courtship and cohabitation durations) associated with each tactic were discussed (Jackson 1978a). In this paper the significance of copulatory behavior in the mating strategy of *P. johnsoni* will be considered.

Although Edwards (1975) reported that males of *Phidippus regius* C. L. Koch may terminate copulation by leaping off the female and running away, this was never witnessed in the case of *P. johsoni*. Instead, copulation was always terminated by the female. For example, females dislodged males by walking or turning in circles, and they drove males away by striking at them with their forelegs, charging toward them, or pushing them (Jackson 1977a).

With respect to the females, the issue of interest is the adaptive significance of variance in how long they tolerate copulating males. This will be a primary concern in Sections III and X. For the male, the question of interest concerns the adaptive significance of prolonged copulation, since each male apparently attempts to copulate for as long as possible. This question will be dealt with especially in Sections IV, V, VI and IX.

General information concerning the maintenance and observation of spiders is provided elsewhere (Jackson 1978a). All statistical tests are described by Sokal and Rohlf (1969); and unless otherwise noted, data are given as means ± S.D.'s. Whenever it was necessary to select spiders for observations in the laboratory, this was usually done randomly (random numbers table, Rohlf and Sokal 1969) or occasionally haphazardly (i.e. with no conscious choice, but not using a random numbers table).

II. PATTERN OF COPULATORY BEHAVIOR

Introduction.—During copulation, both inside and outside nests, the male and female of *P. johnsoni* faced opposite directions with the male's ventral surface against the female's dorsal (mating posture No. 2: Gerhardt and Kaestner 1937). The palpal organs were applied one at a time, the right palp to the right copulatory orifice of the female and

the left palp to the left orifice. While copulating the male leaned to one side of the female, and the female's abdomen rotated 45° to 90°. Between each successive palp application the female's abdomen rotated back to its normal position, and the male tapped and stroked with his legs and palps. Sometimes copulation was interrupted by periods during which the male was not mounted, during which time he might be inactive, groom or perform other activities seemingly not related to communication. However, the majority of the time during which the male was not copulating was spent courting (Jackson 1977a). During transfer of semen, the male's embolus must enter the female's copulatory orifice; but I was unable to observe this during the present study. Consequently, copulation was defined simply as times during which the male's palpal organs were in contact with the epigynum, also referred to as palp "application" or "engagement." Pulsations of the hematodocha occurred throughout the durations of even the longest palp engagements. A single "copulation" was usually comprised of more than one individual application.

Number of Palp Applications.—The number of palp applications per copulation was not related in any simple way to the duration of the copulation or whether the spiders were inside nests. Considering copulations for which numbers of applications were recorded precisely by means of continual observation (Fig. 1), copulations inside and outside nests did not differ greatly (Mann-Whitney U-test, n.s.) in numbers of applications, although copulation durations were very different (means: outside nest, 8.6 min; inside nest, 39.9 min; Mann-Whitney U-test, $P < 0.001$).

Considering copulations observed continuously, it was not unusual for lengthy ones to be accomplished with few palp applications: e.g. 5.85 hr (1 application); 6.00 hr (2); 8.85 hr (4) (each inside nest). Single palp applications lasted from 20 sec to as long as 7.42 hr, with applications lasting 1 or 2 min being common. Although there were copulations lasting 3 min involving 3 applications and 2 min copulations with 2 applications, all copulations lasting 1 min or less included but a single palp application.

Generally only a portion of each copulation following cohabitation was observed. One lasting 18.20 hr was observed in its entirety, during which there were 12 applications (duration for single application: 1-340 min). The maximum number of applications observed during a single copulation was 64 during one following cohabitation that was not observed in its entirety (observed duration: 8.15 hr; estimated: 10 hr).

Duration of Palp Applications.—Durations of individual palp applications followed no obvious rules related to the durations of preceding and following applications, whether palps were applied alternately or repeatedly, whether the application was early or late in the copulation, or whether activity by the female preceded disengagement (Fig. 2).

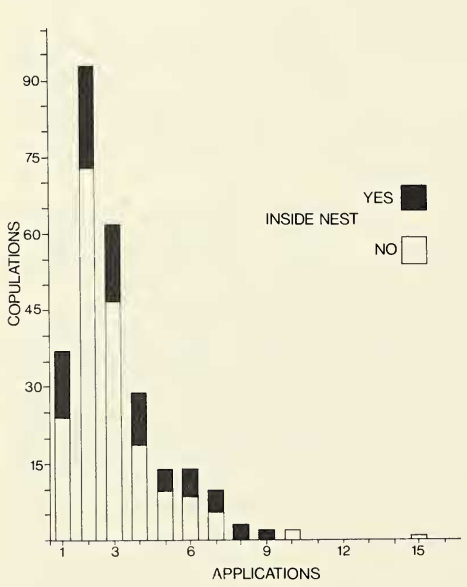
Sequence of Palp Applications.—Considering 923 cases in which males disengaged their palps and then re-engaged, the relative frequency with which the next application was made with the opposite palp was 0.82; that for the same palp was 0.18. The female's behavior was a factor influencing whether the male alternated palps or re-applied the same one. Whenever scraping on the female's abdomen (a component of postmount courtship: Jackson 1977a) followed within a few seconds of palp disengagement, the next engagement was on the opposite side. Sometimes the female's abdomen did not rotate and the male alternately scraped on one side, then the other; and the side on which he finally engaged his palp could be either the same or the opposite from his previous engagement.

Handedness.—There was a tendency for males to favor the left palp when starting to copulate, and there was evidence that individual males were either left or right "handed."

Considering 190 copulations in which the male scraped on only one side of the female's abdomen before the first palp engagement, the first palp applied was the left in 66.8% ($G = 21.985$, $P < 0.005$).

There were 33 males for which the first palp applied was recorded on two successive copulations, with each case preceded by scraping on only one side of the female's abdomen. Twenty applied the same palp first each time (16 left, 4 right). However, these frequencies were not different from those expected from the binomial distribution with equal probabilities for use of each palp. For another set of 15 males, the first palp applied was recorded on 3 successive copulations, with each preceded by scraping on a single side of the female's abdomen. Ten initially applied the same palp during each of the 3 successive copulations (9 left, 1 right). The null hypothesis of equal probabilities for initial use of each palp is rejected ($G = 11.507$, $P < 0.005$). Similar observations were available for 4 successive copulations of only 2 males, and neither initially favored the same palp during each copulation. The significance of "handedness" in the mating behavior of *P. johnsoni* is unclear (see Dill 1977 for a discussion of "handedness" in animals).

Comparison of Copulation with Courtship.—Although it is useful to define courtship as heterosexual communicatory behavior that forms the normal preliminaries to mating (Jackson 1977b), the temptation to assume a clear functional distinction between courtship and copulation can be misleading. For example, the copulatory behavior of the linyphiid spider *Lepthyphantes leprosus* consists of a lengthy first phase during which no sperm is transferred, followed by a shorter phase associated with insemination (van Helsdingen 1965). If the first phase has a communicatory function, it becomes problematic to decide whether this phase should properly be referred to as copulation, courtship, or both. There is increasing evidence that copulatory behavior in animals



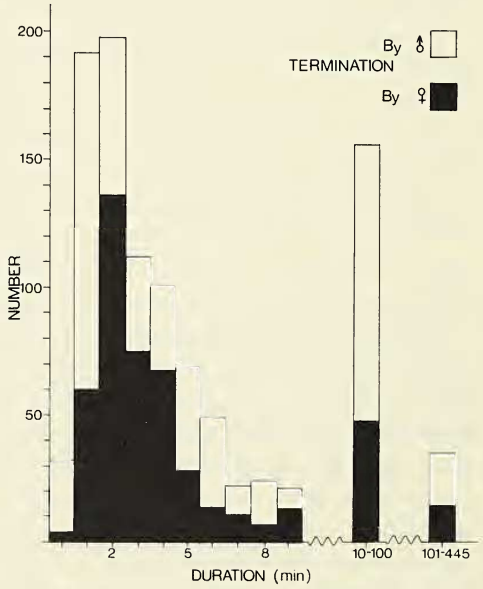


Fig. 1.—Number of copulations during which different numbers of palp applications occurred.

Fig. 2.—Durations of individual palp applications. Terminated by female: female becomes active just before palp removed from epigynum. Terminated by male: female inactive just before removal of palp. 0: 20 sec; 1: 40 sec or 1 min; 2: 2 min; etc.

sometimes serves communicatory functions analogous to courtship. For example, in certain mammals intromission patterns have communicatory functions, promoting fertilization and implantation and possibly enhancing reproductive isolation between species (see Dewsbury 1975).

The copulatory behavior of *P. johnsoni* is highly variable with respect to the number, duration, and sequence of palp applications. The sequence of behavioral units during courtship in *P. johnsoni* is highly variable also; and factors that might favor variability, such as reduction of monotony, have been discussed elsewhere (Jackson 1977a). If copulatory behavior has a communicatory function analogous to courtship, similar selection pressures may promote variability.

III. FACTORS AFFECTING COPULATION DURATION

Introduction and Methods.–Copulation duration was measured as the total time (to the nearest minute) during which the palps were applied, excluding intervening time occupied by other activities. Most copulations were observed virtually continuously; however, for 90 of the very lengthy copulations (Table 1, 1 from row 1; 8, row 2; 81, row 3), there were periods during which the pairs were not under observation, primarily during the dark period in the light regime of the laboratory (12 L: 12 D). One of these copulations took place outside the nest, and it will be discussed separately. The other 89 were inside nests. For each of these, an estimate was made of the fraction of the time spent

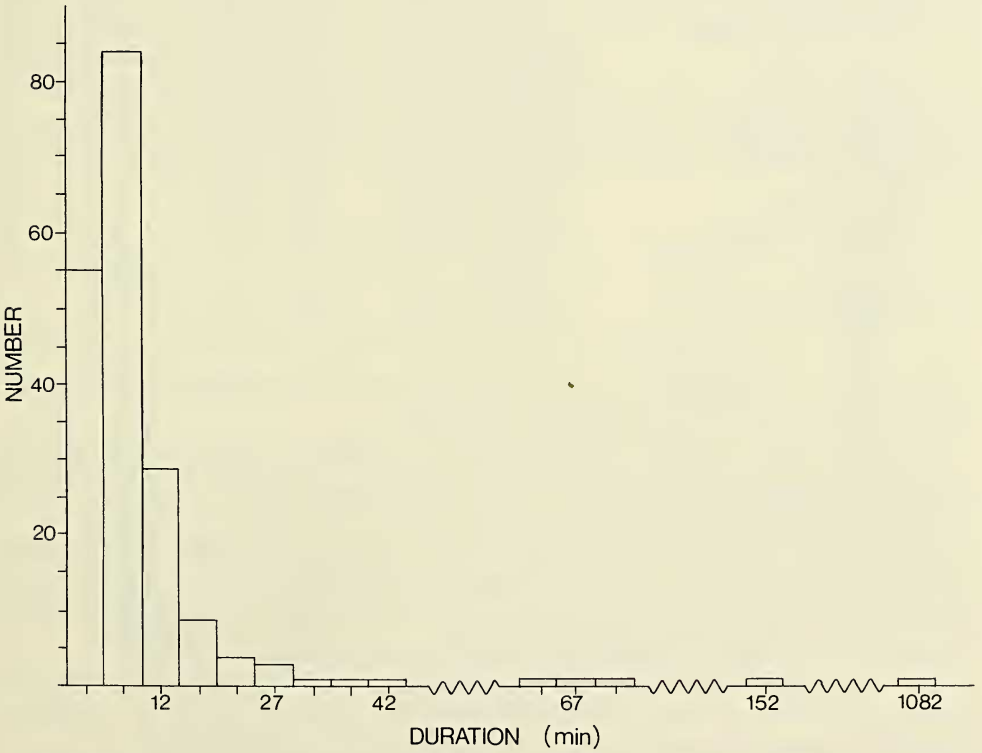


Fig. 3.–Durations of copulations. Female outside nest when encountered by male. 2: 0-4 min; 7: 5-9 min; 12: 10-14 min; etc.

Table 1.—Durations (minutes) of different types of copulations (see text for details concerning each type). Two values for Mean and Max. given when each copulation not observed in its entirety: first, based on estimates; second, only the actually observed portions of each copulation. Outside and Inside: female outside or inside her nest when encountered by male. Cohabit: copulation preceded by cohabitation. Virgin: female's first copulation. Vegetation: copulation took place in presence of vegetation. Red Light: entirety of copulation occurred under incadescent light with red filter. Regular Light: at least part of copulation occurred under fluorescent light with no filter (copulations involving females that molted the same day excluded). Maternal: female inside her nest with eggs. Receptive, Second Day: durations of first copulations of females that were receptive on second day; Gravid: receptive on second day and/or when gravid; Maternal: receptive on second day, when gravid, and/or when maternal (inside and/or outside nest). Unreceptive, Gravid: unreceptive on second day and when gravid; Maternal: unreceptive on second day, when gravid, and when maternal (inside and outside nest). Plug formed: plug present after but not before the copulation. No Plug Formed: plug absent before and after. Enduring Plug: same plug present after at least one later copulation by a different male. Plug Endured and Plug Not Endured: a plug present previous to the copulation and same plug either present or absent afterwards.

Type of Copulation	Mean	Max.	Min.	N
1. Outside	14.13, 8.56	1078, 152	0.33	192
2. Inside, Not Cohabit	109.62, 85.63	1200, 843	0.66	114
3. Inside, Cohabit	863.33, 571.92	2400, 1336	6	89
4. Outside, Virgin, No Vegetation	8.63	152	0.33	109
5. Outside, Virgin, Vegetation	6.16	12	0.33	15
6. Inside, Virgin, Regular Light	51.38, 40.15	1200, 762	2	39
7. Inside, Virgin, Red Light	125.75	531	6	12
8. Inside, Maternal	217.36, 142.12	840, 517	1	25
9. Receptive, Second Day	93.87, 77.71	1680, 1228	0.33	52
10. Unreceptive, Second Day	571.00, 381.96	2400, 1336	1	100
11. Receptive, Gravid	261.48, 186.09	1920, 1228	0.33	49
12. Unreceptive, Gravid	633.79, 431.82	1920, 1158	2	68
13. Receptive, Maternal	341.38, 235.38	1800, 1158	2	21
14. Unreceptive, Maternal	793.33, 535.45	1320, 975	61	9
15. Plug Formed	402.68, 287.21	2400, 1336	1	132
16. No Plug Formed	317.47, 228.57	1680, 1228	0.33	32
17. Enduring Plug Formed	269.52, 188.71	1320, 975	3	21
18. Non-Enduring Plug Formed	247.08, 164.90	2400, 1336	1	48
19. Plug Endured	9.28	70	0.33	22
20. Plug Did Not Endure	123.25, 84.27	1078, 708	1	51

copulating when the spiders were not under observation. This was always less than 0.5, which was likely a conservative estimate in each case.

Observing under red light, I confirmed that *P. johnsoni* copulated during the dark period. In some cases, pairs that had been copulating during the day were checked intermittently during the night (10 checks, ca. 1 hr after the dark period began; 7, 2 hr; 5, 3 hr; 3, 4 hr; 3, 5 hr; 3, 7 hr; 3, 9 hr; 3, 10 hr; 10, 11 hr). The spiders were copulating during 36 of the 47 checks. Another 16 pairs were observed continuously under red light for 3 to 6 hr, and 4 were observed continuously the entire night. These 20 pairs copulated during 85.6 ± 17.20% of the observation period.

For pairs not observed continuously, estimates of copulation durations never more than doubled the recorded copulation durations (observed portion of copulation/ observed + estimated portion: 65.4 ± 8.50%; range, 50.5% - 95.0%; n = 89).

Since data related to copulation duration were not normally distributed, means and ranges, but not standard deviations, will be provided. Each time that estimated copulation

durations were involved, Mann-Whitney U-tests were performed twice, once using estimated values and once excluding the estimated portions of each copulation. The two tests gave consistent results each time.

Type of Female and Her Location.–Copulations during which females were outside their nests tended to be shorter (Fig. 3) than when females were inside nests, the longest usually involving those females that had been cohabiting since the subadult stage (Fig. 4 and 5). Each of the three groups was significantly different from each of the other two (Table 1, rows 1-3; $P < 0.001$).

The longest copulation observed outside a nest began in the early afternoon and ended the following morning. My intermittent observations suggested that the pair copulated continually the entire night. If so, this meant that the copulation lasted 17.97 hr. All other copulations outside nests were observed continuously. None of these took place during the night, and none were nearly as long in duration as this one. The next longest copulations were 152 min, 70 min, and 68 min. All others lasted 31 min or less, usually much less. Why one copulation extended into the night and had an exceptionally long duration is not known.

During most copulations outside nests, the spiders were in essentially bare cages. The 18-hr copulation indicated that lengthy copulations are possible outside nests, raising the question of whether they might be more common under natural conditions in which vegetation, rocks, and other shelter are available. This hypothesis was investigated by observing spiders in field cages and terraria containing vegetation (see Jackson 1977a). All females for these observations were virgins. There was no indication that the presence of rocks and vegetation prolonged copulation (Table 1, compare rows 4 and 5). Also, the spiders copulated wherever they met, showing no tendency to go under shelter. Data for the field cages and terraria, being similar, were pooled.

Reluctance of Female to Depart Nest.–When mating occurred outside nests, bouts of not copulating interspersed within bouts of copulating were shorter and less frequent than when mating took place inside nests (Jackson 1977a). Typically during these

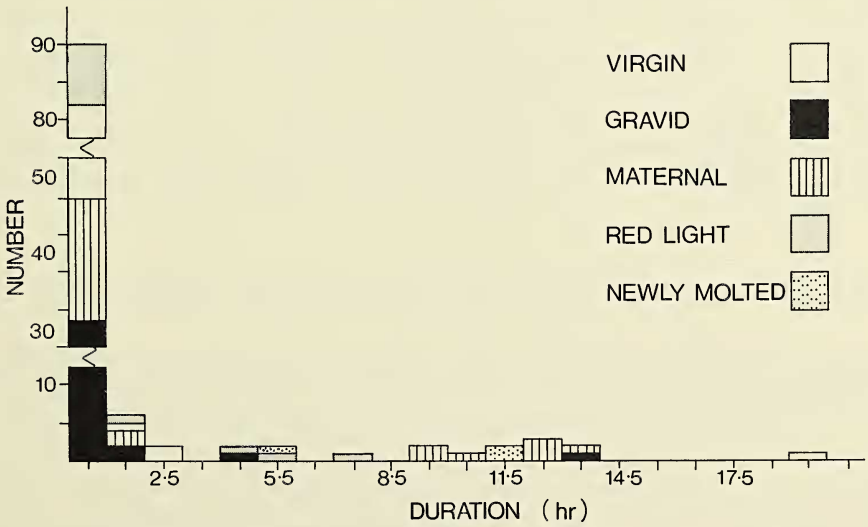


Fig. 4.–Durations of copulations. Female inside nest when encountered by male. Types of females (virgin, gravid, etc.) defined in text. "Virgin" does not include "newly molted" and "red light." 0.5: 0-59 min; 1.5: 60-119 min; 2.5: 120-179 min; etc.

periods, the male repeatedly mounted and stroked the female; but since her abdomen did not rotate, copulation could not take place. Periods of pausing, grooming, or other apparently non-reproductive activities, which sometimes occurred during these periods when the spiders were inside nests, almost never occurred when they were outside.

The minimum number of precopulatory mounts (ones which occurred previous to the male's last palp application) was 1, and any beyond this were interpreted as successful attempts by the male to continue copulation. The mean number of precopulatory mounts when the pairs met outside nests was 1.22, and the maximum was 7. (Observations on the 18-hr copulation were excluded from the calculations here since it was not watched continuously; however, only one mount was observed for this pair.)

The exact number of precopulatory mounts was recorded for 111 pairs that mated inside nests without cohabiting (mean, 2.41; max., 19). More than one precopulatory mount occurred during 49 of these copulations. In contrast, more than one precopulatory mount occurred for only 25 of the 191 pairs that mated outside nests ($\chi^2 = 36.80, P < 0.001$).

The number of precopulatory mounts for pairs mating after cohabitation was comparatively enormous. Based on a sample of 39 pairs, the mean was 27.56 and the maximum was 176. These values were probably gross underestimates since most of these copulations were not observed continuously. In each of these copulations more than one precopulatory mount was observed, compared to only 49 of 111 copulations of non-cohabiting pairs inside nests ($\chi^2 = 34.86, P < 0.001$).

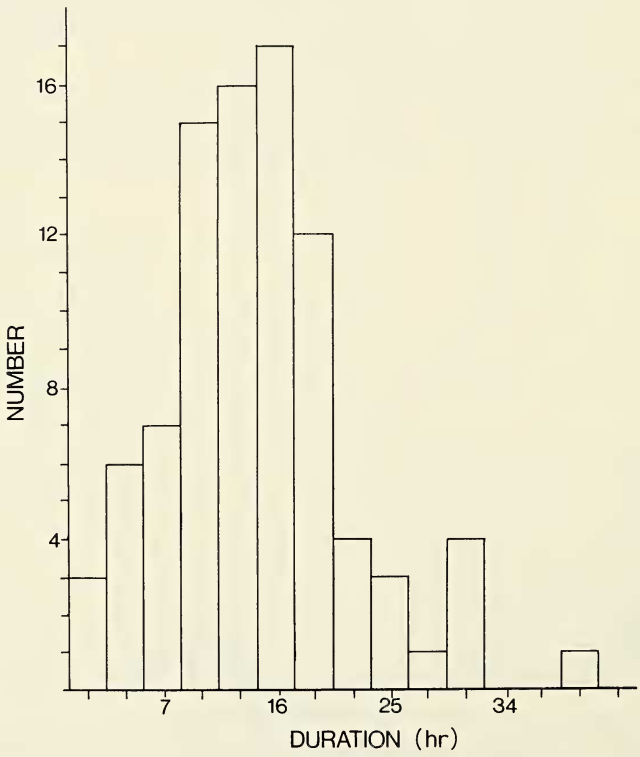


Fig. 5.—Durations of copulations preceded by cohabitation. 1: 0-179 min; 4: 180-359 min; 7: 360-533 min; etc.

These observations suggest a factor that might help explain why copulations tend to be longer when females are inside their nests. Apparently, the female's most effective tactic for terminating copulation is to decamp; but when she is inside her nest, decamping requires at least temporary departure from the nest. Females seem reluctant to depart their nests, and this is most likely related to the value of the nest in protection from predators, as a site for oviposition, etc. The trend in behavior of the female might be the result of an evolutionary compromise in which the advantages of terminating copulation by decamping are weighed against the disadvantages. If the female is outside her nest already, the disadvantages would seem relatively small; and we would predict these females would decamp more readily.

Spiders in individual laboratory cages generally remained in their nests one or more days after molting, and spiders in nature seem to be similar in this respect (Jackson 1979). Perhaps physiological processes, such as cuticle hardening, are optimally carried out inside nests during this period. Whatever the reasons, however, reluctance to depart the nest immediately following molting may account for relatively long copulations following cohabitation. Observations on 3 females that did not cohabit are of interest in relation to this hypothesis. A male was introduced into the cage of each female 1-2 hr after she molted, and each pair mated inside the nest. These copulations lasted 6.05 hr, 11.52 hr, and 11.73 hr. In the case of all other virgin females for which copulation was not preceded by cohabitation, molting occurred at least one day previous to introduction of the male, and copulation duration tended to be shorter (Fig. 4; Table 1, rows 6 and 7; Mann-Whitney U-test, $P < 0.01$).

Phidippus johnsoni almost always remains inside a nest at night, which is not surprising for a vision-dominated, diurnal animal. In a study comparing the sensory modalities employed in types 1 and 2 courtship (Jackson 1977b), females mated inside nests under dim red light, and one would expect these females to be hesitant to depart their nests. It is of interest that these copulations were relatively lengthy when compared with ones that began under regular light (Fig. 4; Table 1, rows 6 and 7; Mann-Whitney U-test, $P < 0.05$).

Female *P. johnsoni* tend to remain in their nests with their eggs, possibly protecting them from parasites and predators; and sometimes they oviposit several successive batches in a single nest (Jackson 1979). One might expect maternal females to be especially reluctant to depart their nests. In the laboratory, females occupying nests with their eggs copulated longer than the largest class of non-maternal females inside nests (virgins, regular light: Fig. 4; Table 1, rows 6 and 8). Since the difference approached but did not reach significance (Mann-Whitney, $0.05 < P < 0.10$), this factor should be investigated further.

IV. RELATIONSHIP BETWEEN COPULATION DURATION AND FERTILITY

Introduction and Methods.–One might expect more sperm to be transferred during longer copulations, resulting in a positive correlation between copulation duration and the number of fertile eggs oviposited by the female. This hypothesis will be considered next.

Virgin males and females (collected as subadults) were assigned to two groups. Each female in the long-copulation group mated on the day she molted after cohabiting with the male (copulation duration: 5-24 hr). Each female in the short-copulation group mated outside the nest within 2 days after molting (copulation duration: 2-8 min, except for one pair which copulated for 29 min). Each male underwent his final molt 5-25 days

previous to copulation, and there was no evidence that the fertility of females was influenced by the age of the males with which they mated. The number of fertile egg batches oviposited was recorded; and for each fertile batch, a record was kept of the number of spiderlings that emerged and the number of eggs that failed to hatch. (For information on oviposition and hatching of eggs, see Jackson 1978b.)

Results and Discussion.—Copulation apparently had an all-or-none, non-graded effect on fertility. Some copulations did not produce fertile eggs. However, if one considers only the fertile matings, there was no relation between how many fertile eggs a female oviposited and whether the copulation lasted a few minutes or several hours. Females in the long-copulation group produced 172.4 ± 46.14 fertile eggs, compared to 192.8 ± 94.92 for the short-copulation group (Table 2). The total number of fertile batches was 3.36 ± 1.29 for the long-copulation group, compared with 3.20 ± 1.30 for the short-copulation group. The long-copulation group produced 71.3 ± 12.45 (n = 11) fertile eggs in the first batch, 60.6 ± 12.49 (n = 10) in the second batch, and 45.6 ± 13.27 (n = 9) in the third. The comparable data for the short-copulation group are 74.4 ± 22.95 (n = 5), 63.5 ± 12.71 (n = 4) and 49.3 ± 13.52 (n = 4).

The all-or-none relationship probably holds for even the shortest copulations. In other studies, females were provided opportunity to mate repeatedly (see Section V). When we consider only the females that copulated only once, despite repeated opportunities, one oviposited fertile eggs after a copulation which included only one palp application lasting 1 min. She oviposited 139 fertile eggs in 2 batches. Although other females oviposited fertile eggs after single copulations of 2-3 min, their eggs were not counted.

There was a consistent trend with respect to whether matings were fertile or not. Each of the 11 females in the long-copulation group, but only 5 of the 10 females in the short-copulation group, oviposited fertile eggs ($\chi^2 = 4.726, P < 0.05$).

Data were available for another 66 females that copulated a single time before ovipositing. Although their eggs were not counted, each was maintained in the laboratory sufficiently long to oviposit at least one batch of eggs (see Jackson 1978b). Of these, 26 copulated 30 min or less; and 40 copulated 5 hr or more. Data from these females were added to the data from the 21 previously discussed females. A total of 19 females were infertile after short copulations; 17 were fertile. In the long-copulation group, all 51 females were fertile ($G = 53.578, P < 0.005$).

V. RELATIONSHIP BETWEEN COPULATION DURATION AND FIDELITY

Introduction.—Although there are numerous exceptions, the general trend among animal species seems to be that males attempt to copulate with many females, whereas females are more discriminating and mate with relatively few males (Bateman 1948). Although this trend probably occurs in spiders, it has not been investigated thoroughly. There are frequent references in the literature concerning males of spiders mating with more than one female. Female spiders are more often, but not always, reported to mate with a single male; however, reports from different researchers on the same species are not always consistent. In *P. johnsoni*, the difference between virgin and non-virgin females was not so simple. Sometimes non-virgin females re-mated, but compared to virgin females they mated less readily.

The probability that a previously mated female will copulate with a second male should be the product of two factors, the frequency with which she encounters courting males and her fidelity to the first male (i.e. whether she refuses to mate again when another male courts her). The relation between fidelity and the duration of the female's first copulation will be considered in this section.

Table 2.–Relationship between copulation duration and oviposition.

Spider	Duration of copulations (min.)	Number of fertile batches	Number of fertile eggs
1	4	4	295
2	6	1	64
3	6	3	180
4	7	4	149
5	8	4	276
6	300	2	158
7	300	4	179
8	480	3	161
9	600	5	213
10	660	3	238
11	840	4	180
12	900	5	189
13	1020	4	195
14	1140	1	67
15	1440	2	122
16	1440	4	194

Terminology.–A *virgin* female is one that has not copulated. A female that has copulated is *non-virgin*, regardless of whether she has been inseminated, a distinction that will be clarified later.

A *second-day* female is one which completed her first copulation 24-48 hr previous to the time of the test in question.

Typically a female feeds voraciously after copulating for the first time. A week or two later, her abdomen is distended, having a width noticeably greater than that of the cephalothorax. These females are defined as *gravid*. Only those gravid females that had not yet oviposited for the first time were considered in this study.

A *maternal* female is one which has recently oviposited fertile eggs.

Methods.–A "test" occurred when a male was placed in the same cage with an adult or subadult female. "Successful tests" were cases in which courtship occurred. Unsuccessful tests were rare. A few successful tests ended when cannibalism occurred. Tests without cannibalism ended when the male became unresponsive to the female, either before or after copulation. An "unresponsive male" was one that neither courted, followed, nor watched the female. When a nest was present, the male was not judged unresponsive until he was no longer in physical contact with a nest containing a female (Jackson 1977a).

All tests were started in the morning or early afternoon. Sometimes a single male was employed in more than one test on a single day, but at least 60 min elapsed between successive tests involving the same male. A male was never tested more than once with the same female on the same day, although he might be randomly selected for testing with the same female on a different day. Once a male copulated, he was not used in further tests on the same day.

In a "test sequence," a female was tested with successive males until she mated or until she had been tested with 4 males, whichever occurred first. A female that mated was defined as "receptive." At least 4 min elapsed between tests in a sequence, usually much more. When a sequence was not completed in one day, it was continued the next day. In the case of females tested in nests, testing was postponed if they departed their nests prior to completion of a sequence. Testing continued on the same day if a female

returned to her nest before late afternoon. Otherwise, testing continued the following morning, since spiders almost invariably occupied nests just after the lights came on in the laboratory (Jackson 1979).

When a female was tested outside a nest, all nests in her cage were destroyed before the first male was introduced. Except for maternal females, females tested outside nests always departed their nests spontaneously prior to nest destruction. Maternal females were forced from their nests with a camel hair brush. When females were tested inside nests, any additional nests in the cages besides the ones being occupied by the females were destroyed prior to introduction of the male.

After a female copulated, whether she was fertile was defined by whether she oviposited fertile eggs. When females died without ovipositing less than 1 month after copulation, no judgment was made as to their fertility.

Each female was subjected to a test sequence on the second day, again when she was gravid, and also when she was maternal. All second-day and gravid females, except those in Set B (see below), were tested outside nests only. Test sequences with gravid females always began at least one week after the sequences on the female's second day. From among the females that were unreceptive when gravid, each of 18 were subjected to another test sequence, outside nests while still gravid, one week after the previous sequence.

After I determined that the female's first batch of eggs was fertile, she was subjected to 2 test sequences after later fertile ovipositions. One of these was with the maternal female inside her nest with her eggs; the other was after a different oviposition, with the female outside her nest. Approximately half the females were first tested inside nests; the other half were first tested outside nests. Test sequences were carried out 2 to 7 days after oviposition. For inside-nest test sequences, the females occupied their nests with their eggs. For outside-nest test sequences, the females were forced from the nests and transferred to clean cages, and the test sequence was carried out ca. 24 hr later in a cage without nests. Eggs of maternal females were kept in glass vials long enough to ascertain their fertility.

Females in Set B were subjected to an abbreviated testing procedure, including test sequences on the second day and while gravid, but not while maternal. The gravid females in this set were tested inside nests.

For various reasons, it was not always possible to carry out all tests for all females. For example, sometimes after one maternal test sequence, the female died, escaped, or failed to oviposit again. All spiders used in this study were collected as immatures in nature, except that some females collected as adults were used as supplementary females in the maternal test sequences. When the supplementary females were collected with fertile eggs, test sequences began after they oviposited their first batch in the laboratory. Ones collected without eggs were not used until after they had oviposited an intervening batch of fertile eggs in the laboratory.

Results and Discussion.—For each reproductive state, both inside and outside nests, there were some females that copulated. Females which copulated for a relatively short time at their first mating were more likely to copulate again on the second day. Looking at this phenomenon in a slightly different way, females that were receptive on the second day copulated for a mean of only 94 min at their first mating, compared to a mean of 571 min for ones that were unreceptive on the second day (Fig. 6; Table 1, rows 9 and 10; Mann-Whitney U-test, $P < 0.001$). Similarly, the first copulation was longer for females that showed fidelity to the first male after tests on both their second day and

while gravid (Fig. 7; Table 1, rows 11 and 12; Mann-Whitney U-test, $P < 0.001$), and for those that showed fidelity during tests on their second day, while gravid, and while maternal (Fig. 8; Table 1, rows 13 and 14; Mann-Whitney U-test, $P < 0.01$). There was no evidence of short term fluctuations in receptivity since the 18 unreceptive gravid females that were tested again a week later remained unreceptive.

A problem in interpreting these data arises. Both copulation duration and pursuit time (Jackson 1979) tended to be much greater for spiders mating inside nests (not preceded by cohabitation) compared to those mating outside, and both tended to be greater still if cohabitation was involved. Possibly, the important factor influencing female fidelity was either pursuit time or simply to which of the three categories the copulation belonged (i.e., outside nest, inside nest without cohabitation, or inside nest with cohabitation). Attempts to ascertain statistically which of these factors was more important, using subsets of the existing data, were inconclusive. However, certain observations gave the impression that the important variable was indeed copulation duration.

Six females that cohabited before mating the first time were receptive on the second day; 63 were not. Two of the receptive females were ones that initially copulated, for unknown reasons, for unusually short periods, 6 min and 85 min. (Each of the other four females copulated 9 hr or longer.) Pursuit time, however, was not unusually short for any of these females (6.2 ± 1.83 days; min., 4 days). Among the females that did not cohabit, 3 initially copulated for ca. 6 hr or longer; all others copulated initially for ca. 2 hr or less. Two of these (copulation durations: 531 min, 351 min) were not receptive on the second day, despite the pursuit times preceding their first copulations being short (8 min

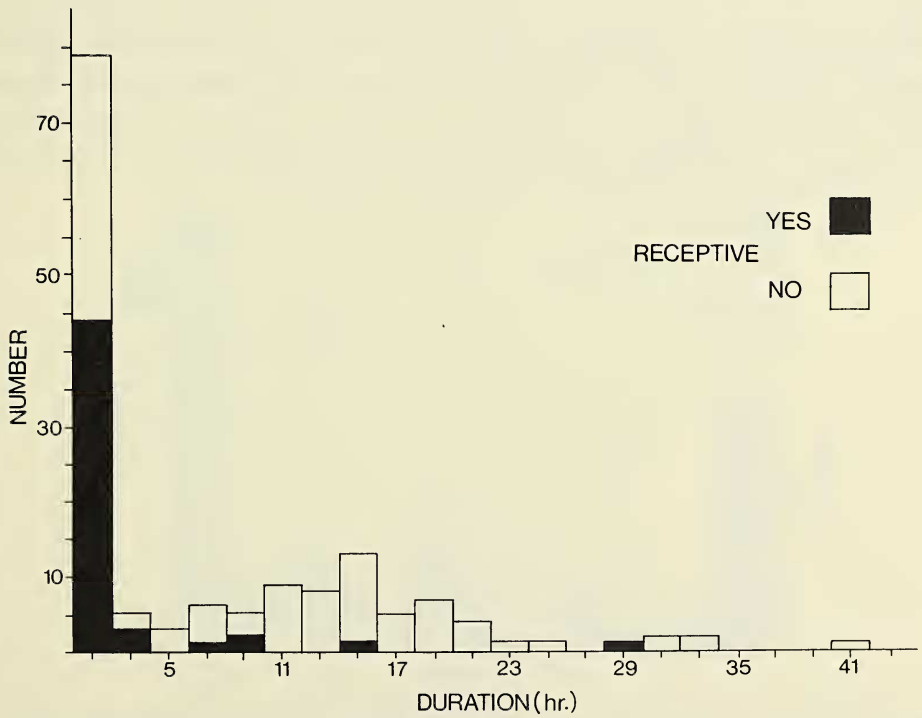


Fig. 6.–Number of copulations of differing durations. First copulation in life of each female. Females tested on second day (see text). Receptive: mated during the test sequence. Unreceptive: failed to mate. 1: 0-119 min; 3: 120-239 min; 5: 240-359 min; etc.

for both). (The other female, receptive on the second day; initial copulation, 378 min; initial pursuit time, 20 min.)

The nest was another factor that seemed to influence receptivity. Females inside nests were more likely to be receptive than females outside. Of the 54 maternal females tested both inside and outside nests, only 7 were receptive while outside nests, compared to 22 that were receptive while inside nests (McNemar test, $\chi^2 = 9.391, P < 0.001$).

In the case of gravid females, the same females were not tested both inside and outside nests. All those tested inside nests while gravid were ones that copulated 20 min or less at their first mating. Of those females tested outside nests while gravid, 77 copulated more than 20 min at their first mating, and these were deleted when the two groups were compared. Only 13 of the remaining 57 females were receptive when tested gravid outside nests. On the other hand, 24 of the 34 females tested inside nests were receptive ($\chi^2 = 18.220, P < 0.001$).

Reluctance of females to depart their nests, a factor discussed earlier with respect to pursuit time (Jackson 1978a) and copulation duration (Section III), may also influence receptivity. Gravid females seem less agile than other females, and this may increase their susceptibility to predators while outside nests. Besides, gravid females inside nests are likely preparing to oviposit, and this may contribute to their reluctance to depart nests. The reluctance of maternal females to leave their nests and eggs has been discussed previously.

To summarize, females of *P. johnsoni* may mate with more than one male. However, the trend seems to be that a female is more likely to mate again if her previous copulation was relatively short. This suggests a selection pressure favoring males with prolonged copulation: males that copulate for relatively long periods may tend to leave their sperm with females that are less likely to mate with other males. To evaluate this hypothesis properly, we need to know the relative frequencies with which females encounter additional courting males after copulations of differing durations. If females behave in such a way as to be equally or less likely to encounter additional males after relatively long copulations, then the proposed hypothesis seems probable.

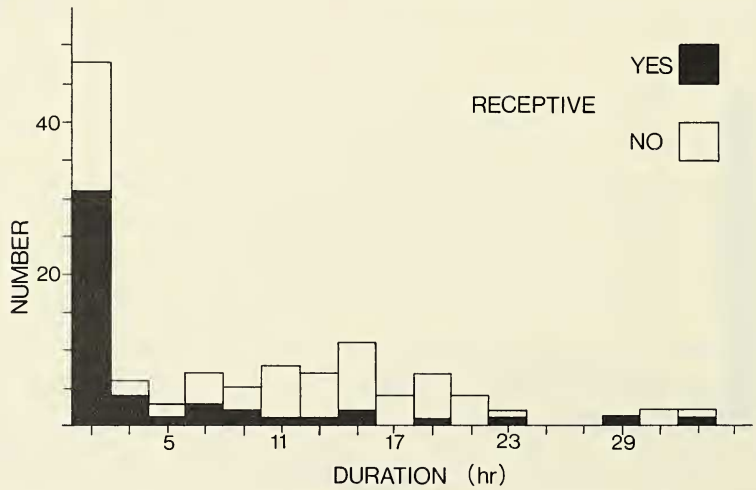


Fig. 7.—Number of copulations of differing durations. First copulation in life of each female. Each female tested on second day and when gravid. Receptive: mated during at least one test. Unreceptive: failed to mate during all tests. 1: 0-119 min; 3: 120-239 min; 5: 240-359 min; etc.

VI. INTERVAL BETWEEN COPULATION AND THE TERMINATION OF FEMALE RECEPTIVITY

Introduction.–After copulation, females of the mosquito *Aedes aegypti* become unreceptive to additional males; however, there is an interval of several hours between insemination and the termination of female receptivity (Craig 1967). It seemed important to determine whether a latency of this sort occurs in *P. johnsoni*. For a species in which there is a latency between insemination and the onset of female unreceptivity, natural selection might favor males that prolong copulation until the end of the latency period. Sperm competition would be reduced as a result of monopoly of the female by the male during the period when additional males might displace his sperm. I designed an experiment to investigate this in *P. johnsoni*.

Methods.–Twenty virgin females each copulated for 35 min or less. For Group A (10 females), a test sequence was begun immediately after the end of the first copulation and completed within 1 hr. Each female in Group B was subjected to a test sequence 8 to 9 hr after the end of the first copulation. All females were subjected to yet another test sequence ca. 24 hr after the initial copulation in order to ascertain the consistency of fidelity over this period. All test sequences were carried out with the females outside nests. All spiders were collected as subadults.

Results and Discussion.–Five of the 10 females in Group A copulated with a second male when tested within 1 hr of the initial copulation. Virtually the same proportion of females in Group B (6 of 10) copulated with a second male when tested 8 to 9 hr after the initial copulation. Only three females changed their state of receptivity when tested the second day.

Earlier (Section V) it was shown that 53% of 38 females that initially copulated outside nests were receptive on the second day, consistent with the results in this study

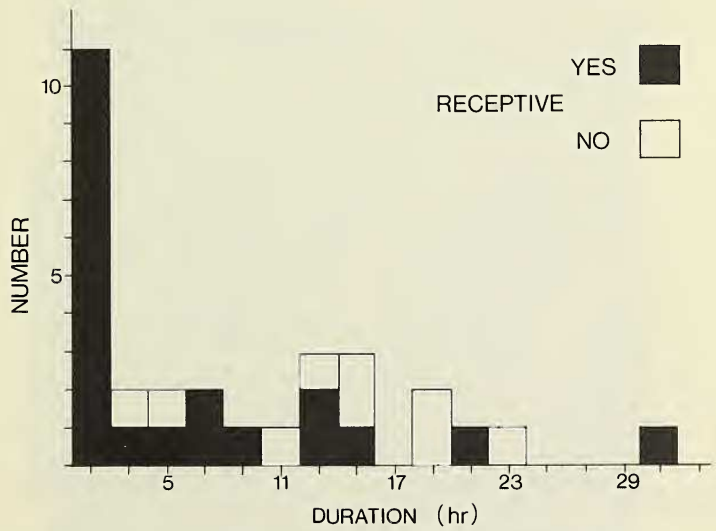


Fig. 8.–Number of copulations of differing durations. First copulation in life of each female. Each female tested on second day, when gravid, and when maternal, inside and outside nest (see text). Receptive: mated during at least one test. Unreceptive: failed to mate during all tests. 1: 0-119 min; 3: 120-239 min; 5: 240-359 min; etc.

for females tested within 1 hr, between 8 and 9 hr after, and ca. 24 hr after their initial copulation. Apparently, if the female becomes unreceptive after mating, the effect is virtually immediate.

VII. MATING PLUGS

Introduction.—After mating, the copulatory orifices of the females of *P. johnsoni* were frequently covered by a white, yellow, orange, or red substance which I referred to as the "mating plug." (These never covered the orifices of virgin females.) No two plugs were exactly alike in size, shape, color, and texture. One or, more often, both orifices on the epigynum were covered. Gonopores were never covered. The material of the plug was sometimes concentrated over the orifices with the area between more sparsely covered. Sometimes the area between was completely uncovered, and the plug consisted of 2 discrete units. Other times, the plug was a large mass covering both orifices with no conspicuous differentiation into 2 parts. Asymmetries were common, with more material over one of the 2 orifices. Plugs varied from a fine film to a bulky mass. Usually they had a grainy appearance, but some were smooth and shiny. In some cases, plugs assumed the shape of wedges within the orifices. More often, they were highly sculptured, amorphous masses of material. A single plug could have components of varied color, texture, size, and shape (Fig. 9).

Mating plugs have been reported for other groups of spiders, including some Clubionidae, Oxyopidae, Thomisidae, Toxopidae, and Theridiidae (Brady 1964, Exline and Whitcomb 1965, Forster 1967, Muniappan and Chada 1970, Whitcomb and Eason 1965). In some araneid, oxyopid, and theridiid spiders, parts of the male's palpal organ are found embedded as plugs in the copulatory orifices of the female after mating (Abalos and Baez 1963, Bhatnagar and Rempel 1962, Brady 1964, Kaston 1970, Levi 1969, Robinson and Robinson 1978).

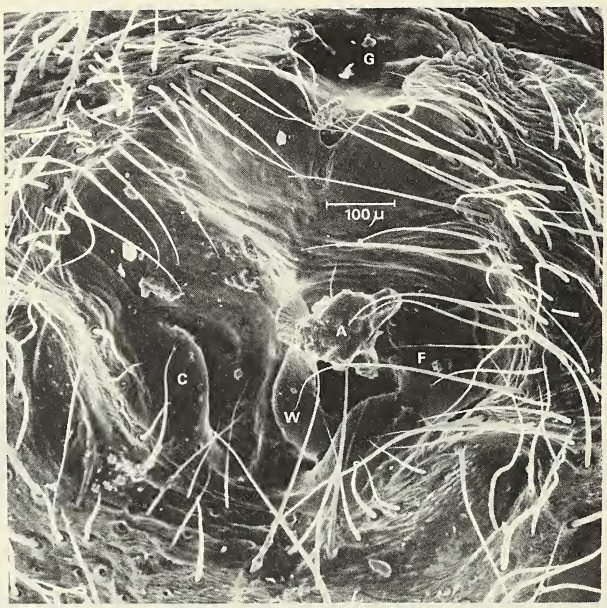


Fig. 9.—Epigynum (S.E.M.) of *Phidippus johnsoni*. C: copulatory orifice. Plug, over one copulatory orifice, in 3 forms (A: amorphous mass, F: film, W: wedge situated in orifice). G: gonopore.

Functions of plugs related to reduction of sperm leakage and to sperm competition (hindrance of insemination by additional males) both might be involved (see Parker 1970); the latter will be considered here for the plugs of *P. johnsoni.*

Methods.–Concurrently with the study of fidelity (Section V), females were checked for plugs. Checks were made within 12 hr after virgin females copulated and within 24 hr after later copulations. Females in Set B were not checked. Dry ice, which produces low temperatures and carbon dioxide gas, was used to anesthetize the spiders for 1-2 min while they were examined under a microscope.

Whenever a plug was present, it was described and a sketch was made. Evidently, plugs did not change in appearance spontaneously. A second examination of 24 females occurred when they died 2-5 mo after their last copulations. Another 20 females that were not involved in the study of fidelity were examined within 24 hr after their first copulation and again 2 weeks later, without having mated again. Of these 44 females, 24 had plugs at the later examinations that matched the descriptions of their previous plugs; the other 20 lacked plugs at both examinations.

Results and Discussion.–On 74 occasions males copulated with females that already had plugs from previous copulations. Afterwards, either a different plug or no plug was present in 52 cases. In the other 22 cases the previous plug was still present, indicating that it had protected the previous male's sperm investment; and in 2 of these cases a plug endured 2 subsequent copulations. These data suggest that plugs are effective ca. 30% of the time. However, since only the exteriors of genitalia were examined, a substantial part of the plug might not have been visible; and 30% effectiveness might be an underestimate. Another consideration is that a male may sometimes alter the previous male's plug, possibly add a plug of his own, but fail to insemination the female.

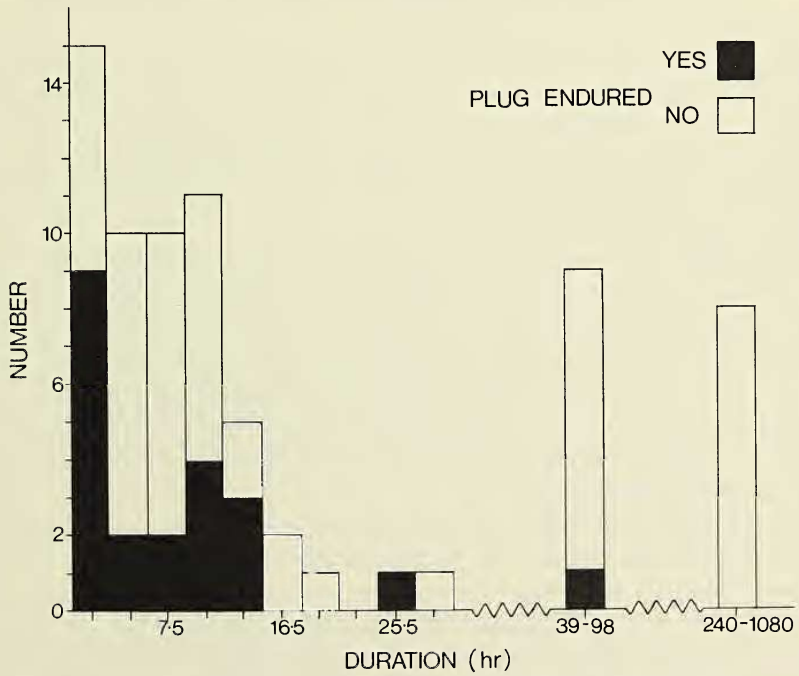


Fig. 10.–Number of copulations of differing durations. Plug present previous to copulation. Endured: same plug present after the copulation. Did not endure: different or no plug present after the copulation. 1.5: 0-179 min; 4.5: 180-359 min; 7.5: 360-539 min; etc.

Considering females initially lacking plugs, both virgins and non-virgins, there was no evident relation between whether a plug formed and copulation duration (Table 1, rows 15 and 16). However, the possibility of internal plugs must be kept in mind.

There was also no evident relation between the duration of the copulation just previous to formation of the plug and whether the plug endured succeeding copulations (Table 1, rows 17 and 18), but there was a relation between plug endurance and the succeeding copulation. Considering copulations involving females already possessing plugs, copulations after which the previously present plug endured tended to be much shorter than those after which plugs did not endure (Fig. 10; Table 1, rows 19 and 20; Mann-Whitney U-test, $P < 0.01$).

In conclusion, plugs seem to be adaptations related to sperm competition in *P. johnsoni*. If a male leaves a plug on the female's copulatory orifices after mating, then his sperm investment is protected to some extent even if the female is receptive to additional males. The plug forms a physical barrier that a second male must overcome before he can copulate with the female and displace the first male's sperm. This probably requires a variable but substantial proportion of the duration of the second male's copulation. One can manually push plugs off the genitalia of anesthetized females by using an insect pin. Perhaps the male physically displaces the plug in a similar way using structures on his palp. This suggests that when plugs endured second copulations, females tolerated the presence of males for a time insufficient for them to displace plugs left by earlier males. When males mate with non-virgin females, the time required to displace plugs may be one of the factors favoring males that copulate for prolonged periods.

VIII. RELATIONSHIP BETWEEN FERTILITY AND FIDELITY

Introduction.—As shown in the study of female fertility (Section IV), all females did not oviposit fertile eggs after a short copulation. In the study of female fidelity (Section V), it was shown that females were more likely to be receptive after a short copulation than after a long one. These two observations suggested the hypothesis that the mated females which were receptive were ones that could not oviposit fertile eggs from the previous copulation alone.

Methods.—Each of 18 virgin females copulated 16 min or less. Within 12 hr afterwards, their copulatory orifices were covered by Eastman 910 Adhesive (Tennessee Eastman Co., Kingsport, Tennessee). These females will be referred to as "cemented." Cemented females were not prevented from ovipositing since their gonopores were not covered, but they could not be inseminated again. When they oviposited, any sperm that fertilized their eggs came from the first copulation even if they had been receptive to additional males. There were 10 "control females." Each was cemented when still virgin and permitted to "mate" the following day.

With the anesthetized spider inverted under a microscope, her copulatory orifices lay in a basin at the anterior end of her epigynum. The adhesive was taken into a microcap (Drummond Scientific Co.). When the microcap was brought briefly into contact with the anterior epigynum, a drop of adhesive filled the basin and covered the copulatory orifices. Using an insect pin, I spread the adhesive evenly in the basin, and pressed the long setae near the anterior of the epigynum into the adhesive. The spider was kept under anesthesia for an additional 5 min while the adhesive dried. Any plugs present on the epigynum were rapidly dissolved by the adhesive.

Results and Discussion.–Apparently, the adhesive effectively prevented insemination. Each control female lived well beyond the normal preoviposition period, and none oviposited fertile eggs. "Copulatory behavior" of males with cemented females was not greatly different from normal. Sometimes they scraped their palps on the epigynum for relatively prolonged periods, but each eventually held his palp stationary against the epigynum, with the hematodocha pulsating.

Eleven mated cemented females were receptive to additional males; 7 were not. Five of the receptive ones oviposited fertile eggs, indicating that receptive females included ones with fertile sperm from previous copulations. This was not consistent with my original hypothesis.

A related hypothesis can be considered. Although fertile females may be either receptive or unreceptive, one might expect all infertile females to be receptive. However, 2 of the infertile females were unreceptive. One might expect that at least a greater proportion would be receptive than unreceptive, but there was no indication of this either (G-test of independence, n.s.).

Another consideration is that although some fertile females were receptive, perhaps they carried fewer stored sperm compared to unreceptive fertile females. However, this hypothesis is not supported by available data either. The 5 fertile receptive females oviposited a mean of 119 ± 32.1 fertile eggs. The 5 fertile unreceptive females oviposited a mean of 145 ± 52.1 fertile eggs (t-test, n.s.). Evidently female receptivity is not simply related to an insufficient quantity of stored sperm.

IX. CONSEQUENCES OF REPEATED COPULATION

Introduction and Methods.–After copulating with one male, a female may be fertile and yet copulate with another male (Section VIII), creating conditions for sperm competition. The loss suffered by the first male should be a product of the probability that the female will mate with other males and the consequences of any additional matings that occur. The probability of repeated mating was discussed in Section V. This section will be concerned with the consequences; i.e., the proportion of the female's eggs fertilized by each male. The sterile male technique has been frequently used in similar studies with insects (Parker 1970). The female mates with two males, one with sterile and one with fertile sperm. Sterility can be induced by hybridization, chemosterilants, or irradiation. Eggs which hatch are attributable to the fertile male. A certain percentage of a female's eggs may normally fail to hatch after a copulation with a fertile male, but any increase beyond this percentage is attributable to the sterile male.

Using a Machlett X–Ray Machine (Picker X-Ray Corp., Cleveland, Ohio) with a beryllium window, two groups of adult male *P. johnsoni* were subjected to x-radiation (dose rate, 17.5 rads per sec): Group A, 10 krad; Group B, 30 krad. During irradiation, each spider was in an individual container (ca. 20 x 12 mm) made from 2-mm-thick plastic tubing, stoppered at each end with cotton. All spiders were irradiated on the same day.

Each irradiated male mated with two virgin females outside nests, the control and the experimental. Each control female mated with an irradiated male only, and her eggs were monitored to ascertain the male's sterility. Each experimental female mated first with an irradiated male and later with a normal male. Each group of irradiated males was divided into two subgroups. For one, mating took place on the second and third day after irradiation; for the other, on the ninth and tenth day. When gravid, each female was

subjected to test sequences (Section V) with normal males, until one of the two females corresponding to each irradiated male mated. The other female became the control.

Results and Discussion.—There was no indication that male longevity, health, or behavior was affected by irradiation. All control females were infertile, indicating that both 10 krad and 30 krad are sublethal sterilizing dosages for *P. johnsoni*, with effects that persist at least 19 days. Data from all groups and subgroups will be pooled for the following discussion.

That irradiation did not render males aspermic was confirmed by examining eggs of control females. Embryos formed from these eggs, but each died at an early stage of development. Irradiation probably caused dominant sublethal mutations in sperm, as generally occurs when this technique is used with insects (Smith and Borstel 1972).

The copulations of irradiated males were all short (19.0 ± 16.53 min; max., 76 min). Although females sometimes fail to oviposit fertile eggs after short copulations with fertile males (Section IV), it is extremely unlikely that this alone accounts for the infertility of the 29 control females.

Of the 22 experimental females, 12 were infertile. Apparently in these cases the second male was unsuccessful at displacing any of the first male's sperm. The females in this study were not examined for plugs, but it seems likely that some irradiated males left plugs which blocked the second males' attempts to inseminate the females.

Normally, after mating with a fertile male, the mean proportion of eggs which hatch decreases as the female oviposits successive batches (Jackson 1978b). In 6 cases the hatch proportions of experimental females in this study were similar to those for normal females for each batch they oviposited. Apparently the second male completely displaced the irradiated male's sperm in these cases.

The hatch proportions for the first batches of each of the remaining 4 females (0.0408, 0.1127, 0.6290, 0.6667) were compared individually with the first batch hatch proportions of normal females (0.89 ± 0.085): t-values were 9.351, 8.558, 2.451, and 2.866, respectively; $P < 0.05$ for each.

Apparently these were cases in which the second male's sperm only partially displaced that of the first male. The spiders in this study were not maintained long after their first batch. However, one oviposited a second batch, and the hatch proportion was similar to that for second batches of normal females. Studies designed to look at sperm utilization in later batches are needed.

To summarize, three different consequences were associated with a second male copulating with a previously mated female: failure to displace any of the first male's sperm (55% of the cases), partial displacement (18%), and total displacement (27%). Since larger sample sizes and reversal of the sequence of mating (females mating with normal males first; irradiated males second) might alter estimates of these frequencies, the qualitative conclusion will be emphasized. The male's losses through female infidelity are potentially large in *P. johnsoni*, since his sperm may be partially or totally displaced when the next male copulates. Males that reduce such losses by prolonging copulation should be favored by natural selection.

X. MECHANISMS CONTROLLING FEMALE RECEPTIVITY AND THEIR ADAPTIVE SIGNIFICANCE

Although the mechanisms by which copulation induces unreceptivity in *P. johnsoni* are unknown, studies of insects provide some suggestions. In some Diptera, sperm or

other substances ("matrone" or "accessory material") originating from the male reproductive tracts induce unreceptivity in females (Leopold 1976). In *Musca domestica* prolonged copulation is linked to mechanisms inducing female unreceptivity. Copulation generally lasts ca. 1 hr, yet virtually all sperm transfer occurs during the first 10 to 15 min (Murvosh *et al.* 1964). During the remaining time, transferral of accessory material takes place. Perhaps something similar occurs in *P. johnsoni*, although accessory substances have not yet been looked for in spiders. If the female's unreceptivity is positively correlated with the quantity of accessory material transferred, this might in turn be correlated with the duration of copulation. A quantitative effect of this sort would seem to be the case in *M. domestica* (Leopold *et al.* 1971, Riemann and Thorson 1969).

In some insects there is evidence that female unreceptivity is induced by mechanical stimuli concurrent with copulation (Obara *et al.* 1975, Truman and Riddiford 1974). It would be of interest to look for tactile receptors associated with the epigynum of *P. johnsoni*, and a relationship between the quantity of stimulation received and the probability that the female will be unreceptive. Such stimulation might act on the female's central nervous system by either a neural or endocrine pathway, both of which have been implicated in insects. However, since the onset of female unreceptivity is sometimes virtually instantaneous, a neural pathway seems more likely in *P. johnsoni.*

Often in insects one male at one copulation can completely fill the female's sperm storage capacity (Parker 1970), and this seems likely for *P. johnsoni* also. There is no indication in *P. johnsoni* that the number of fertile eggs oviposited is increased when the female copulates more than once. Also the male's sperm remains viable in the female's spermathecae for many months. Mating might expose females to increased predation risks (Jackson 1976). Time involved in supernumerary copulations might be optimally used for other activities, such as feeding, nest building, etc. Considering these factors alone, one would predict natural selection to favor females that become unreceptive after a single insemination. This raises questions concerning the ultimate causes of mechanisms by which female fidelity is linked with copulation duration.

In a variable or unpredictable environment, it may be that the females that increase the variance of their progeny by copulating with more than one male might have a selective advantage over females that mate with only one male (Williams 1975). Because of three considerations, this hypothesis seems inadequate for *P. johnsoni.* Although repeated mating occurs, it seems relatively infrequent; and when it occurs, sperm mixing is not the rule. However, the main difficulty is that this hypothesis provides no apparent explanation for the linkage of fidelity and copulation duration.

If the female's tactics for ridding herself of a persistent male are relatively ineffective, she may run greater risks of predation and waste more time by resisting rather than by copulating. This factor, which can be considered as a form of rape (Parker 1974), was discussed earlier in reference to the relatively great receptivity and copulation duration of females occupying nests. Rape in the more literal sense of copulation with continually resisting females apparently does not occur in *P. johnsoni.* The difficulty with this hypothesis, as with the previous, is that it provides no apparent explanation for the linkage of fidelity and copulation duration at the previous mating.

Short copulations are apparently more likely to be infertile. Suppose the female cannot detect the presence of sperm. This might lead to selection pressure favoring females that are less likely to show fidelity to a male after a short rather than a long copulation. By mating again these females may significantly increase the chances that they will be fertile.

In many habitats, other *Phidippus* species occur sympatrically with *P. johnsoni*, and reproductive isolation is another factor that might be important in relation to female fidelity. Relatively long copulations might be less likely with heterospecific males. Copulation itself might not persist long if the male is of a different species; and a less direct, but perhaps more important, consideration may be that longer copulations tend to be associated with longer precopulatory associations. During the relatively long courtships when females occupy nests and especially during the very long associations when pairs cohabit, there may be a significantly greater probability that heterospecific pairs will fail to copulate because the female and/or the male make species discriminations. (For similar arguments concerning birds, see Mayr 1970). Although the duration of the precopulatory association might be of greater relevance than copulation duration, copulation duration might be more readily measured by the female.

XI. CONCLUSION

It is often tempting to envisage the courtship of animals as variable among species but essentially uniform within species. This portrayal was found to be misleading for the courtship of *P. johnsoni* (Jackson 1977a). The courtship of this species encompasses many elements of behavior, some of which occur only rarely; and the sequence in which they occur during interactions varies greatly. In addition to complexity of this type, precopulatory behavior is organized into two distinct types of courtship and three alternative mating tactics.

Copulatory behavior is also complex in *P. johnsoni*; and as with precopulatory behavior, consideration of the alternative mating tactics is crucial in understanding variation in copulatory behavior. For example, there is no simple answer to questions concerning the typical duration of copulation in this species. Copulation duration in *P. johnsoni* varies over almost the entire range known for the animal kingdom, but there is a trend related to mating tactics: copulation is short with females outside nests, longer with females inside nests, and very long after cohabitation.

Variation in copulatory behavior highlights another question that is frequently viewed as misleadingly simple, namely the function of copulation. Certainly, transfer of sperm as a preliminary to fertilization is a major function, but the present study has illustrated the need to consider sperm competition and other functions.

ACKNOWLEDGEMENTS

For his valuable assistance during all phases of this study, I thank Roy Caldwell. I thank Mary Catharine Vick, Lyn Forster, Simon Pollard, Jerome Rovner, and Susan Riechert for their comments on the manuscript and Lennell Allen for operating the scanning electron microscope. Thanks go to H. T. Mortimer for assistance with the sterilization procedure. For assistance in the laboratory and for valuable discussions, I thank C. E. Griswold, E. I. Schlinger, C. L. Allen, G. W. Barlow, W. Loher, J. Matsui, K. Evans, Z. T. Halpin, M. L. Reaka, L. K. Johnson, and H. T. Gordon.

LITERATURE CITED

Abalos, J. W. and E. C. Baez. 1963. On spermatic transmission in spiders. Psyche, 70:197-207.
Bateman, A. J. 1948. Intra-sexual selection in *Drosophila*. Heredity, 2:349-368.

Bhatnagar, R. D. S. and J. G. Rempel. 1962. The structure, function, and post-embryonic development of the male and female copulatory organs of the black widow spider *Latrodectus curacaviensis* (Müller). Canadian J. Zool., 40:465-510.

Brady, A. R. 1964. The lynx spiders of North America, north of Mexico (Araneae: Oxyopidae). Bull. Mus. Comp. Zool., Harvard, 131:429-518.

Bristowe, W. S. 1958. The world of spiders. Collins, London. 304 pp.

Corbet, P. S. 1964. Observations on the swarming and mating of mosquitoes in Uganda. Proc. Roy. Soc. London, A 39:15-22.

Craig, G. B. 1967. Mosquitoes: female monogamy induced by male accessory gland substance. Science, 156:1499-1501.

Dewsbury, D. A. 1975. Diversity and adaptation in rodent copulatory behavior. Science, 190:947-954.

Dill, L. M. 1977. 'Handedness' in the Pacific tree frog (*Hyla regilla*). Canadian J. Zool., 55:1926-1929.

Edwards, G. B. 1975. Biological studies on the jumping spider, *Phidippus regius* C. L. Koch. M.S. Thesis, University of Florida, Gainesville. 64 pp.

Exline, H. and W. H. Whitcomb. 1965. Clarification of the mating procedure of *Peucetia viridans* (Araneida: Oxyopidae) by a microscopic examination of the epigynal plug. Florida Entomol., 48:169-171.

Forster, R. R. 1967. The spiders of New Zealand Part I. Otago Mus. Bull., 1:1-124.

Gerhardt, U. and A. Kaestner. 1937. Araneae, pp. 394-656. In W. G. Kükenthal (ed.) Handbuch der Zoologie, Vol. 3. DeGruyter, Berlin.

Hartnoll, R. G. 1969. Mating in the Brachyura. Crustaceana, 16:161-181.

Jackson, R. R. 1976. Predation as a selection factor in the mating strategy of the jumping spider *Phidippus johnsoni* (Salticidae, Araneae). Psyche, 83:243-255.

Jackson, R. R. 1977a. An analysis of alternative mating tactics of the jumping spider *Phidippus johnsoni* (Araneae, Salticidae). J. Arachnol, 5:185-230.

Jackson, R. R. 1977b. Courtship versatility in the jumping spider *Phidippus johnsoni* (Araneae: Salticidae). Anim. Behav., 25:953-957.

Jackson, R. R. 1978a. The mating strategy of *Phidippus johnsoni* (Araneae, Salticidae): I. Pursuit time and persistence. Behav. Ecol. Sociobiol., 4:123-132.

Jackson, R. R. 1978b. The life history of *Phidippus johnsoni* (Araneae, Salticidae). J. Arachnol., 6:1-29.

Jackson, R. R. 1979. Nests of *Phidippus johnsoni* (Araneae, Salticidae): characteristics, pattern of occupation, and function. J. Arachnol., 7:47-58.

Kaston, B. J. 1970. Comparative biology of American black widow spiders. Trans. San Diego Soc. Nat. Hist., 16:33-82.

Leopold, R. A. 1976. The role of male accessory glands in insect reproduction. Ann. Rev. Entomol., 21:199-221.

Leopold, R. A., A. C. Terranova, B. J. Thorson, and M. E. Degrugillier. 1971. The biosynthesis of the male housefly accessory secretion and its fate in the mated female. J. Insect Physiol., 17:987-1003.

Levi, H. W. 1969. Problems in the reproductive physiology of the spider palpus. Bull. Mus. Nat. Hist. Nat., Paris, Suppl. 1, 41:109-111.

Mayr, E. 1970. Populations, species, and evolution. Belknap/Harvard University Press, Cambridge, Massachusetts. 453 pp.

Muniappan, R. and H. L. Chada. 1970. Biology of the crab spider, *Misumenops celer*. Ann. Entomol. Soc. America, 63:1718-1722.

Murvosh, C. M., R. L. Fye, and G. C. LaBrecque. 1964. Studies on the mating behavior of the house fly, *Musca domestica* L. Ohio J. Sci., 64:264-271.

Nayar, K. K. 1958. Studies on the neurosecretory system of *Iphita limbata* Stal. V. Probable endocrine basis of oviposition in the female insect. Proc. Indian Acad. Sci., 47:233-249.

Obara, Y., H. Tateda, and M. Kurabara. 1975. Mating behavior of the cabbage butterfly, *Pieris rapae crucivora* Boisduval. V. Copulatory stimuli inducing changes of female response patterns. Dobut. Zasshi, 84:71-76.

Parker, G. A. 1970. Sperm competition and its evolutionary consequences in insects. Biol. Rev., 45:525-567.

Parker, G. A. 1974. Courtship persistence and female-guarding as male time investment strategies. Behaviour, 48:157-184.

Richards, O. W. 1927. Sexual selection and allied problems in the insects. Biol. Rev., 2:298-364.

Riemann, J. G. and B. J. Thorson. 1969. Effect of male accessory material on oviposition and mating by female houseflies. Ann. Entomol. Soc. America, 62:828-834.

Robinson, M. H. and B. Robinson. 1978. The evolution of courtship systems in tropical araneid spiders. Symp. Zool. Soc. London, 42:17-29.

Rohlf, F. J. and R. R. Sokal. 1969. Statistical tables. Freeman, San Francisco. 253 pp.

Smith, R. H. and R. C. Borstel. 1972. Genetic control of insect populations. Science, 178:1164-1174.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. Freeman, San Francisco. 776 pp.

Syrjamaki, J. 1966. Dusk swarming of *Chironomus pseudothummi* Strenzke (Dipt.: Chironomidae). Ann. Zool. Fenn., 3:20-28.

Truman, J. W. and L. M. Riddiford. 1974. Hormonal mechanisms underlying insect behavior. Adv. Insect Physiol., 10:297-352.

Unwin, E. E. 1920. Notes upon the reproduction of *Asellus aquaticus*. J. Linn. Soc. London, (Zool.) 34:335-343.

Van Helsdingen, P. J. 1965. Sexual behaviour of *Lepthyphantes leprosus* (Ohlert) (Araneida, Linyphiidae), with notes on the function of the genital organs. Zool. Mededel., 41:15-42.

Whitcomb, W. H. and R. Eason. 1965. The mating behavior of *Peucetia viridans* (Araneida: Oxyopidae). Florida Entomol., 48:163-167.

Williams, G. C. 1975. Sex and evolution. Princeton University Press, Princeton, New Jersey. 200 pp.

Manuscript received March 1979, revised September 1979.